

Phaeocollybia chefensis* sp. nov. and new synonyms for *P. riffipes*, *P. rufotubulina*, and *P. tibiikauffmanii

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ABSTRACT—Phylogenetic analyses of ITS and RBP2 sequence data from *Phaeocollybia* collections made at Cascade Head Experimental Forest in Oregon support recognition of a new species, *P. chefensis*. Collections of the new species were previously referred to *P. tibiikauffmanii*. Sequence analyses also establish that *P. tibiikauffmanii* is a synonym of *P. spadicea*, *P. riffipes* is a synonym of *P. lilacifolia*, and *P. rufotubulina* is a synonym of *P. californica*. A revised general key to Pacific Northwest *Phaeocollybia* species is provided.

KEY WORDS—*Basidiomycota*, *Hymenogastraceae*, nomenclature, Northwest Forest Plan, taxonomy

Introduction

Phaeocollybia R. Heim (*Agaricomycetes*, *Hymenogastraceae*) is a genus of brown-spored agarics characterized by conic-campanulate pilei, cartilaginous stipes and pseudorhizae, ornamented ‘beaked’ basidiospores, sarcodimitic tissue, monovelangiocarpy, and tibiiform diverticula that arise from the mycelium and primordial pellicular remnants (Norvell 1998a,b; Norvell & Exeter 2009). The forests of western North America have provided an exceptionally large number of species in this genus (Murrill 1911; Smith 1937, 1957a,b; Smith & Trappe 1972; Redhead & Norvell 1993; Norvell 1998a,b,

2000, 2002, 2004; Norvell & Redhead 2000, Norvell & Exeter 2007, 2009; Norvell & al. 2010).

In 1995 the first author collected a solitary tawny colored *Phaeocollybia* from Oregon's Cascade Head Experimental Forest (CHEF). Although the specimen's general morphology resembled that of *P. kauffmanii* (A.H. Sm.) Singer, it differed by possessing abundant refractive tibiiform cheilocystidia, prompting application of the provisional name *P. tibiikauffmanii* to the Oregon coast taxon in Norvell's 1998 doctoral dissertation.

The author's research on *Phaeocollybia* coincided with establishment of the Northwest Forest Plan (NWFP; USDA-USDI 1994), which listed 14 phaeocollybias among its 234 fungal species of concern (Castellano & al. 1999, 2003; ORBIC 2021). In 1998 transects were established for surveying epigeous ectomycorrhizal basidiomycetes in Benton County's Bureau of Land Management (BLM) Green Peak Density Management Study and Polk County's BLM Fungal Chronosequence Study (Norvell & Exeter 2004). Numerous gregarious to caespitose clusters of *P. kauffmanii*-like specimens with tibiiform cheilocystidia were collected that matched the solitary 1995 specimen from Lincoln County. After morphological comparison with other specimens from Washington, Oregon, and California, a particularly well-documented collection from the chronosequence 'old growth' study transect (approximately 64 km from the CHEF site) was selected as type for *P. tibiikauffmanii* (Norvell 2004).

In 2008, the U.S. Forest Service (FS) & BLM Interagency Special Status/Sensitive Species Program initiated a project to generate DNA sequence data for *Phaeocollybia* specimens (Gordon 2009). Since then, 350 sequences for the internal transcribed spacer region (ITS1-5.8S rRNA-ITS2) in the nuclear ribosomal RNA gene cassette and 46 sequences of a portion of the gene encoding the second largest subunit in the DNA-directed RNA polymerase (RPB2) were deposited in GenBank. These data, along with NWFP surveys, have provided several hundred *Phaeocollybia* collections for taxonomic and genetic analysis, and serve as an excellent resource for phylogenetic analyses and specific primer design.

Initial molecular analyses that clustered *P. tibiikauffmanii* and *P. spadicea* sequences within one intermixed clade were received on the same day as the arrival of the galley proofs for *PHAEOLLYBIA OF PACIFIC NORTHWEST NORTH AMERICA* (Norvell & Exeter 2009). Although the vital data arrived too late for a thorough publication revision, the authors annotated their keys and commentaries in anticipation of subsequent taxonomic changes.

Additional ITS sequence analyses confirmed the synonymy of *P. spadicea* and *P. tibiikauffmanii* but also supported newly collected material from the original Lincoln County ‘*tibiikauffmanii*’ site as a distinct species, independent of *P. spadicea*.

A revised ITS-based phylogeny of *Phaeocollybia* was presented in the Norvell & al. (2010) poster at the International Mycological Congress in Edinburgh. In this paper we provide additional ITS and RPB2 sequence data that establish *P. cheffensis* as a new species and formally publish synonymies for *P. californica* (= *P. rufotubulina*), *P. lilacifolia* (= *P. riffliipes*), and *P. spadicea* (= *P. tibiikauffmanii*).

Materials & methods

Collections

Specimen collection and examination, ultraviolet inspection, and syringaldazine spot tests of fresh material followed procedures outlined in Norvell & Exeter (2009), where morphotaxonomic terms (e.g., tibiiform diverticula, sarcodimitic tissues, pellicular veil, vertical-monopodial, and rhizomorphic pseudorhizae) are also defined. Parenthesized color references from Ridgway (1912: e.g., “Pale Pinkish Cinnamon”) accompany colors of fresh specimens described in general non-standardized color names in lower case. Microscopical examinations were made of fresh tissues in H₂O or (for the type material) dried tissues rehydrated in 6% aqueous KOH. Basidiospores were taken from the stipe apex. Dimensions of all anatomical cells follow the format n (number measured): (outlier)low–average–high(outlier) [e.g., basidia n = 19: 25–34.2–41(43) × 6.5–8.1–9.4(9.9) μm].

Collector abbreviations include LLN (Norvell), RLE (Exeter), and SAR (Redhead). Latitude/longitude geographic coordinates were converted and rounded to four decimal places from surveyor input using [for TRS] <https://www.earthpoint.us/TownshipsSearchByDescription.aspx> and [for UTM] <https://www.ngs.noaa.gov/NCAT/>.

Vegetation abbreviations follow those used during Northwest Forest Plan surveys and include (in all caps for overstory) ABPR (*Abies procera* Rehder), PISI (*Picea sitchensis* (Bong.) Carr.), PSME (*Pseudotsuga menziesii* (Mirbel) Franco), and TSHE (*Tsuga heterophylla* (Raf.) Sarg.) and (in small caps for understory) BENE (*Berberis nervosa* Pursh = *Mahonia nervosa* (Pursh) Nutt., the preferred synonym), GASH (*Gaultheria shallon* Pursh), OXOR (*Oxalis oregana* Nutt.), POMU (*Polystichum munitum* (Kaulf.) C. Presl), VAOV (*Vaccinium ovatum* Pursh), and VAPA (*Vaccinium parviflorum* Andrews = *Gaylussacia baccata* (Wangenh.) K. Koch, the preferred synonym).

Material cited in the SPECIMENS EXAMINED sections is housed (unless otherwise specified) in Norvell’s Pacific Northwest Mycology Service fungarium (PNW) and will be distributed among DAOM, NY, OSC, PNW, and WTU after publication. Herbarium acronyms follow Thiers (2021).

TABLE 1: PNW *Phaeocollybia* ITS & RPB2 sequence data. (Type data in bold).

SPECIES	COLL./FUNG. NUMBER	ITS	RGB2	COUNTY, STATE/PROV; PRIMARY COLLECTOR
<i>ammirati</i>	LLN1941028-10-T	JN102495	—	Clackamas, OR; Norvell
	LLN2051018-01	GQ165629	—	Skamania, WA; Norvell
	OSC 155802	KJ450913	—	Coos, OR; Rodenkirk
	RLE2007-103	(GQ165627)	KU574760	Benton, OR; Exeter
	RLE2007-105	GQ165624	KU574759	Polk, OR; Exeter
	RLE2008-068	KX574502	—	Benton, OR; Exeter
	RLE2009-19	JN102493	KU574787	Benton, OR; Exeter
	RLE2009-31	JN102494	KU574790	Benton, OR; Exeter
	RLE2009-41	KX574503	—	Benton, OR; Exeter
<i>attenuata</i>	LLN2071029-51	JN102501	—	Benton, OR; Norvell
	RLE2007-026	MZ352106	KU574794	Lincoln, OR; Exeter
	RLE2007-090	JN102498	—	Benton, OR; Exeter
	RLE2007-176	(GQ165632)	KU574761	Benton, OR; Exeter
<i>benzokauffmanii</i>	LLN1921120-01-T	GQ165636	—	Mendocino, CA; Norvell
	RLE2007-035	GQ165636	—	Benton, OR; Exeter
	RLE2009-15	(JN102502)	KU574785	Benton, OR; Exeter
<i>californica</i>	MICH 11607-T	JN102503	—	Del Norte, CA; Smith
	OSC 109290	EU669240	—	Linn, OR; Smith
	OSC 109332	EU846292	—	Josephine, OR; Friend
	RLE2007-177	GQ165647	KU574764	Benton, OR; Exeter
	RLE2010-05	JN102504		Benton, OR; Exeter
#	LLN1921116-1 ruf-T	GQ165707	—	Mendocino, CA; Norvell
#	SAR7500	GQ165708	—	Mendocino, CA; Redhead
<i>chefensis</i>	RLE2009-04-T	MZ352102	KU57484	Lincoln, OR; Exeter
	LLN2091026cc6a	MZ352101	—	Benton, OR; Norvell
	OSC 155803	MK326851	—	Polk, OR; Christensen
	RLE2007-074	MZ352097	KU574779	Lincoln, OR; Exeter
	RLE2007-129	MZ352096	—	Lane, OR; Exeter
<i>dissiliens</i>	OSC 114217	EU846271	—	Coos, OR; Sperling
	RLE2008-138	KF219569	KU574767	Benton, OR; Exeter
<i>fallax</i>	LLN1921007-01	JN102512	—	Vancouver Isl. BC; Redhead
	RLE2004-01	JN102511	—	Benton, OR; Exeter
	RLE2007-140	MZ352103	KU574791	Benton, OR; Exeter
	RLE2007-159	JN102516	KU574795	Benton, OR; Exeter
	RLE2007-175	JN102518	KU574796	Benton, OR; Exeter

SPECIES	COLL./FUNG. NUMBER	ITS	RGB2	COUNTY, STATE/PROV; PRIMARY COLLECTOR
<i>gregaria</i>	LLN2091026cg8	JN102520	—	Benton, OR; Norvell
	RLE2007-061	GQ165652	—	Lincoln, OR; Exeter
	RLE2008-026	GQ165654	KU574772	Polk, OR; Exeter
	RLE2013-07b	KJ450915	—	Polk, OR; Exeter
<i>kauffmanii</i>	LLN1931015-02	JN102542	—	Clallam, WA; Leuthy
	RLE2006-10	KF219573	KU574782	Benton, OR; Exeter
	RLE2006-13	JN102547	—	Benton, OR; Exeter
	RLE2007-095	JN102524	—	Polk, OR; Exeter
	RLE2008-027	KF219572	KU574781	Polk, OR; Exeter
	RLE2008-045	JN102526	—	Lane, OR; Exeter
<i>lilacifolia</i>	LLN1921111-06	KF219576	—	Clackamas, OR; Norvell
	LLN2071018-12	GQ165657	KU574763	Lincoln, OR; Exeter
^	RLE2006-43	KF219580	—	Polk, OR; Exeter
^	RLE2013-44	—	KU574803	Lane, OR; Exeter
<i>luteosquamulosa</i>	LLN2071029-33	GQ165668	KU574774	Benton, OR; Norvell
	LLN2071029-43	GQ165667	—	Benton, OR; Norvell
	RLE2007-016	GQ165663	—	Lincoln, OR; Exeter
	WTU-F-003084	JN102528	—	Snohomish, WA; Ammirati
<i>ochraceocana</i>	RLE2007-033-T	GQ165674	KU574775	Polk, OR; Exeter
	OSC 134678	GQ165672	—	Benton, OR; Villella
	OSC 134679	GQ165671	—	Tillamook, OR; Paque
	RLE2007-009	GQ165673	—	Polk, OR; Exeter
<i>olivacea</i>	LLN1921015-03	JN102533	—	Jefferson, WA; Norvell
	LLN1921122-04	JN102530	—	Mendocino, CA; Norvell
	LLN1941128-01	JN102532	—	Clackamas, OR; Norvell
	OSC 109501	EU846281	—	Coos, OR; Sperling
	OSC 113875	EU846282	—	Douglas, OR; Kersens
	RLE2007-122	JN102534	KU574798	Benton, OR; Exeter
	RLE2007-133	JN102535	KU574799	Lane, OR; Exeter
	RLE2008-050	MZ352094	KU574766	Lane, OR; Exeter
	RLE2008-051	JN102536	—	Benton, OR; Exeter
	RLE2008-129	GQ165678	KU574776	Benton, OR; Exeter
<i>oregonensis</i>	LLN2001105-01	GQ165681	—	Multnomah, OR; Norvell
	OSC 67425	EU846273	—	Douglas, OR; Goldenberg
	RLE2006-16	GQ165685	—	Lane, OR; Exeter
	RLE2013-42	—	KU574804	Lane, OR; Exeter

SPECIES	COLL./FUNG. NUMBER	ITS	RGB2	COUNTY, STATE/PROV; PRIMARY COLLECTOR
<i>phaeogaleroides</i>	RLE199-064a-T	OM065392	—	Benton, OR; Exeter
	RLE2009-29a	MF737171	KU57489	Benton, OR; Exeter
	RLE2010-086	KX574499	—	Benton, OR; Exeter
<i>piceae</i>	MICH 11629-T	MF737169	—	Tillamook, OR; Smith
	RLE2007-178	(MZ352093)	KU574762	Mendocino CA; Bojantchev
	RLE2009-12	KF219583	—	Benton, OR; Exeter
<i>pleurocystidiata</i>	LLN1940330-02-isoT	GQ165688	—	Clallam WA; Norvell
	LLN1930516-01	GQ165686	—	Linn, OR; Bailey
	RLE2008-002	GQ165687	KU574765	Benton, OR; Exeter
<i>pseudofestiva</i>	LLN1921104-10	KF219588	—	Multnomah, OR; Norvell
	RLE2007-069	KF219589	KU574797	Lincoln, OR; Exeter
	RLE2007-070	KF219590	—	Lincoln, OR; Exeter
<i>radicata</i>	OSC 112980	EU846275	—	Coos, OR; Rodenkirk
	RLE2006-19	GQ165696	—	Benton, OR; Exeter
	RLE2008-131	GQ165695	KU574771	Benton, OR; Exeter
<i>redheadii</i>	LLN2071018-17	JN102544	—	Lincoln, OR; Norvell
	LLN2091026cg18	JN102541	—	Benton, OR; Norvell
	RLE2007-106	JN102546	—	Polk, OR; Exeter
	RLE2008-038	MZ352098	KU574783	Lincoln, OR; Exeter
<i>scatesiae</i>	LLN1921015-19	GQ165701	—	Jefferson, WA; McClenaghan
	LLN1931104-09	GQ165703	—	Lincoln, OR; Norvell
	LLN2071029-02	GQ165699	KU574768	Benton, OR; Norvell
	RLE2007-151	GQ165700	KU574769	Benton, OR; Exeter
<i>sipei</i>	LLN1971023-69	EU644706	—	Benton, OR; Norvell
	OSC 96908	EU644707	—	Linn, OR; Bacheller
	RLE2007-123	GQ165704	KU574773	Benton, OR; Exeter
<i>spadicea</i>	OSC 112482	EU697252	—	Benton, OR; Giachini
	OSC 113791	EU669364	—	Douglas, OR; Wetzel
	OSC 134542	MZ352099	—	Douglas, OR; Sperling
	RLE2009-18	JN102550	KU574786	Benton, OR; Exeter
	RLE2009-20	JN102551	KU574788	Benton, OR; Exeter
*	A2011031ox1 tib-T	KF219597	KU574780	Polk, OR; Norvell
*	A2061114o2-O	KF219596	KU574778	Polk, OR; Norvell
*	RLE2007-165	(KF219594)	KU574777	Benton, OR; Exeter
<i>P. sp. 1</i>	OSC 155805	JN102507	KU574793	Lane, OR; Loring
	RLE2010-05	JN102504	—	Benton, OR; Exeter
	RLE2014-01	KU574726	KU574801	Benton, OR; Exeter

SPECIES	COLL./FUNG. NUMBER	ITS	RGB2	COUNTY, STATE/PROV; PRIMARY COLLECTOR
<i>P. sp. 2</i>	RLE2009-09	KX574498	—	Benton, OR; Exeter
	RLE2010-109	KX575400	—	Benton, OR; Exeter
<i>P. sp. 3</i>	LLN2071029-53	(KF219598)	KU574770	Benton, OR; Norvell
	RLE2007-100	KX574493	—	Polk, OR; Exeter
	RLE2007-152	KF219600	—	Benton, OR; Exeter
	RLE2015-35	KU574725	KU574800	Benton, OR; Exeter
<i>P. sp. 4</i>	RLE2010-009	MZ352104	KU574792	Benton, OR; Exeter
	RLE2015-01	KX574505	—	Benton, OR; Exeter
	RLE2015-06	KU574727	KU574802	Benton, OR; Exeter
<i>P. sp. 5</i>	OSC 155806	MF957115	—	Josephine, OR; Scelza
	RLE2013-14	KJ450918	—	Benton, OR; Exeter
<i>P. sp. 6</i>	OSC 134575	GQ165677	—	Linn, OR; Nakvasil
	OSC 151647	MH819350	MH823881	Douglas, OR; Scelza

= *P. rufotubulina*, ^ = *P. rifflipes*, and * = *tibiikauffmanii* in Norvell (1998ab, 2002, 2004) and Norvell & Exeter (2004, 2007, 2009). (T = type); ITS sequences enclosed in parentheses not included in FIG. 1.

DNA amplification & sequencing

Standard protocols and published primers were followed for DNA extraction, PCR amplification, and sequencing (White & al 1990, Gardes & Bruns 1993, Liu & al. 1999, Matheny 2005). Amplifications of the ITS region from 350 *Phaeocollybia* collections representing 34 putative species utilized fungal primers ITS1 and ITS4b (Gardes & Bruns 1993). Amplifications of the RPB2 gene region from 46 collections representing 26 putative species utilized the degenerate basidiomycete specific primers bRPB2-6F and bRPB2-7.1R (Matheny 2005). Additionally, a new RPB2 forward primer, RPB2Phf (5'-GCAGAAACACCYGAGGGC-3', slightly downstream from the bRPB2-6F primer) was designed based on existing *Phaeocollybia* RPB2 sequences and used successfully where the original primer pair failed after multiple attempts. In total 396 (350 ITS + 46 RPB2) new sequences were generated. Additional ITS and RPB2 sequences were added from GenBank to provide a comprehensive phylogeny for *Phaeocollybia* (Norvell & al. 2010, this publication). TABLE 1 provides collection and sequence data for PNW specimens, and TABLE 2 provides sequencing information for extralimital taxa and the outgroup cited in FIGS 1 and 2.

Separate gene regions were initially aligned with Clustal X (Thompson & al. 1997). Subsequent new sequences were aligned manually in MacClade 4.0 (Maddison & Maddison 2000). Taxa for which gene regions were not sequenced were coded as missing. Sequences were aligned using MAFFT ver. 7 (Katoh & al. 2019) and manually corrected using MEGA X 10.0.0 (Kumar & al. 2018, Stecher & al. 2020). All new sequences were deposited in GenBank.

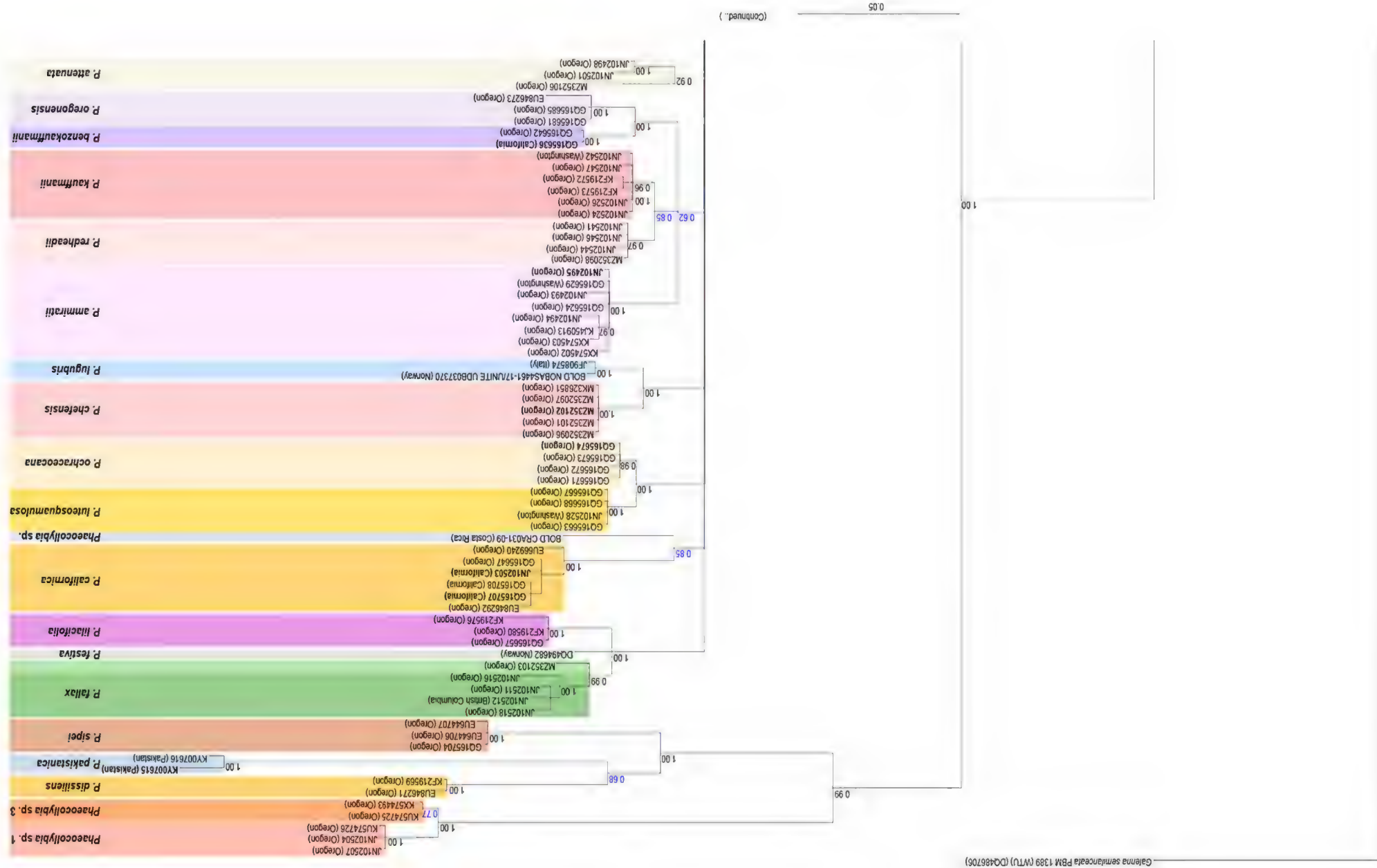


TABLE 2: Sequences from extralimital *Phaeocollybia* spp. and outgroup used in phylogenetic analyses

SPECIES	FUNGARIUM #	GENBANK #	COUNTRY
<i>christinae</i>	MCVE 3539	JF908573	Italy
<i>cidaris</i>	O-F-252891	UDB036543	Norway
<i>elegans</i>	PDD 72723	KY827313	New Zealand
<i>festiva</i> (ITS)	WTU-F-053245	DQ494682	Norway
— (RPB2)	WTU-F-053245	AY509118	Norway
<i>gracilis</i>	PDD 88665	KY827314	New Zealand
<i>graveolens</i>	PERTH 5311586	AF501567	Australia
<i>lugubris</i>	O-F-253794	UDB037370	Norway
	MCVE 14619	JF908574	Italy
<i>megalospora</i>	SP 445402	KC662116	Brazil
<i>pakistanica</i> -T	SWAT 15-1560	KY007615	Pakistan
	SWAT 15-1561	KY007616	Pakistan
<i>ratticauda</i>	PDD 72678	KY827316	New Zealand
	PDD 72544	KY827315	New Zealand
<i>tenuis</i>	PDD 72672	KY827318	New Zealand
<i>Phaeocollybia</i> sp.	TRTC 157723	BOLD CRA031-09	Costa Rica
	AAM A1064	KF041417	Mexico
	PDD 71198	KY827317	New Zealand
<i>Galerina</i>	WTU-F-007080	DQ486706	Washington USA
<i>semilanceata</i>			
(RPB2 gene)	WTU-F-007080	AY337357	Washington USA

All sequences represent the ITS region unless otherwise indicated.

Sequence analyses

Sequences were analyzed using programs available in Geneious Prime (version 2021.2.2). Sequence data were obtained from NCBI and compiled into a multiple sequence alignment. The original ITS dataset contained 296 sequences identified as *Phaeocollybia* spp. Duplicate sequences were removed. Representative sequences for each taxon were retained and the final dataset, including the outgroup, comprised 129 unique sequences. Sequences were trimmed to remove the CATTA and GACCT motifs. For the analysis of partial RPB2 gene sequences, the dataset was composed of 49 unique sequences.

Sequences were aligned automatically using the Geneious alignment tool, and the alignment was refined manually. Phylogenetic analyses were carried out using the MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) plugin developed in Geneious. The following parameters were used: substitution model GTR; rate variation gamma; gamma categories 4; 5 million generations; subsampling frequency 1000; burnin

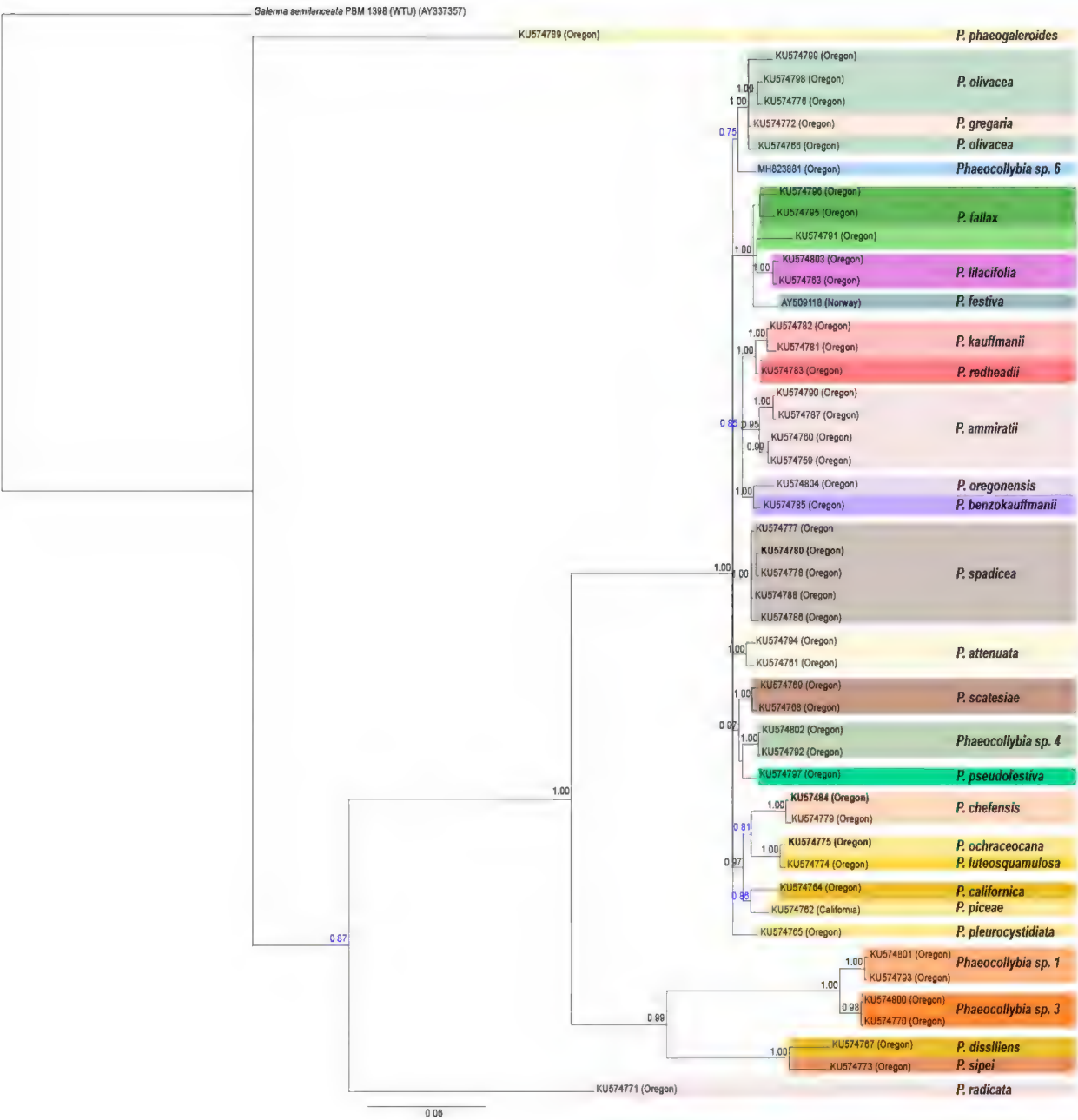


FIG. 2. Phylogenetic analysis of the partial RPB2 gene region in strains of *Phaeocollybia* spp. Branch lengths were determined using the Bayesian consensus outfile. Nodes with posterior probability values <0.90 are indicated in blue. Type strains are indicated in bold.

frequency 50%; heated chains 4; heated chain temperature 0.2; unconstrained branch lengths GammaDir (1, 0.1, 1, 1); and shape parameter exponential (10). The outgroup was *Galerina semilanceata* PBM 1398 (WTU); DQ486706 for the ITS analysis and AY337357 for the RPB2 analysis, respectively). Phylogenetic trees were drawn using the Bayesian consensus outfile and annotations were added using Inkscape 0.92.4.

Phylogenetic results

FIGS 1–2

Norvell & al. (2010) presented the first comprehensive ITS phylogeny for the genus based on 300 *Phaeocollybia* sequences (including two from Australia—*P. graveolens* B.J. Rees & K. Syme, *P. ratticauda* E. Horak—and *P. festiva* (Fr.)

R. Heim from Norway) and the outgroup—*Hebeloma radicosum* (Bull.) Ricken, *Psilocybe semilanceata* (Fr.) P. Kumm., *Galerina marginata* (Batsch) Kühner—revealing a cohesive clade of 69 putative taxa with the *Galerina*-like *P. phaeogaleroides* clade in the basal-most position within *Phaeocollybia*. The current ITS tree (pruned to eliminate duplicates) confirms the existence of three synonymies, several difficult species complexes, and six unnamed species (FIG. 1). The three synonymies supported are *P. riffliipes* = *P. lilacifolia* (>99.7% similarity), *P. rufotubulina* = *P. californica* (>99.5% similarity), and *P. tibiikauffmanii* = *P. spadicea* (>99.8% similarity) (FIGS 1, 2).

The comprehensive ITS phylogeny (not shown) generated from 296 sequences (plus the outgroup *Inocybe pallidicremea* Grund & D.E. Stuntz [as *I. lilacina* (Peck) Kauffman]) and *Galerina semilanceata* (Peck) A.H. Sm. & Singer) and the trimmed 129-sequence ITS tree (FIG. 1) both support 29 PNW species and 14 extralimital putative taxa. A familial relationship between *Phaeocollybia* and *Galerina* is also supported, with both genera now classified in *Hymenogastraceae* (Matheny & al. 2006, Kalichman et al. 2020).

The successful amplification of far fewer (46) RPB2 sequences prohibits generating a robust multigene consensus tree. Nevertheless, both ITS (FIG. 1) and RPB2 (FIG. 2) trees support the same clades. With insufficient coverage across the genus for 28S sequence data and with the two-gene phylogeny well supported by convincing morphological characters, we do not include a 28S-based phylogeny at this time.

Taxonomy

***Phaeocollybia chefensis* Norvell & Exeter, sp. nov.**

FIGS 3–6

IF 559441

Differs from *Phaeocollybia kauffmanii* by its tibiiform cheilocystidia and from *P. spadicea* by its uniformly carrot orange to orange-tawny coloration, larger basidiospores, and solitary to scattered (never gregarious or cespitose) habit.

TYPE: Oregon, Lincoln County, Cascade Head Experimental Forest, W of Hwy 12, 30 m S Tillamook Co. line, 45.0447°N 123.9153°W, 245 m asl, 27.x.2009, *Tsuga heterophylla* (old and young), *Picea sitchensis*, *Vaccinium parviflorum*, *Polystichum munitum*, RLE2009-04 (holotype OSC 155804, isotype PNW; GenBank MZ352102, KU574784).

ETYMOLOGY: derived from the acronym (CHEF) for the type locality, Cascade Head Experimental Forest.

PILEUS 70–80 mm diam, broadly conic-campanulate with acute papillate umbo, upturned inner margin, down-turned outer margin, and straight edge; glabrous, glutinous in rain with the gluten at times somewhat milky, non-striate, overall brownish orange or foxy brown (Tawny, Orange Cinnamon); dried



Ron Exeter

FIG. 3. *Phaeocollybia chefensis* (Holotype, RLE2009-04). TOP: excavated specimens with intact vertical monopodial pseudorhizae. BOTTOM: Two views of the type collection in situ in Cascade Head Experimental Forest, Lincoln County, Oregon. Five collections of 1–2 specimens were collected from this same site during 1995–2021.

pileus uniformly copper metallic. CONTEXT ~6 mm at the disc and confluent with stipitipith, pale orangish white. ODOR faintly floral with farinaceous overtones; TASTE mild, not distinctive. LAMELLAE nearly free, ventricose, thin with $\pm$ even edges, polydymous with 3–7 irregularly interspersed tiers of lamellulae, narrow (4–5 mm, with average length/width ratio 5.5), close, pale orangish buff (Warm Buff) when young, developing darker spots in maturity. VEIL sparse (when present, evident only as occasional darker fibrillose

remnants on stipe apex). STIPE slightly eccentric, terete, 80–90 mm above ground level, overall length including pseudorhiza ≤ 200 mm, apex 10–12 mm diam, $\pm$ equal above, gradually narrowing below toward pseudorhiza; glabrous except for occasional fibrils, moist, finely longitudinally lined, apex pale to deep pinkish orange (Pinkish Cinnamon, Orange Cinnamon) below grading to dull pinkish brown (Fawn Color), 2 mm thick cartilaginous rind surrounding compact fibrillose orangish white stipitipith, rind sometimes with small perpendicular separations producing ~ 5 mm long recurved rind patches. PSEUDORHIZAL FORM vertical-monopodial, $\leq 2/3$ overall stipe length, gradually tapering to pale salmon-colored pointed to blunt origin, firm pith brown where water-soaked, otherwise concolorous with stipitipith. SPORES IN MASS dull pinkish brown (Fawn Color).

BASIDIOSPORES ($n = 64$): $8\text{--}8.9\text{--}10 \times (5)5\text{--}5.6\text{--}5.8 \mu\text{m}$, $Q = (1.45)1.52\text{--}1.65\text{--}1.81(1.84)$, limoniform with a protruding beaked apex in profile, fusoid-elliptical to amygdaliform in face view, apical callus $0.5\text{--}1 \mu\text{m}$ long (occasionally abrupt or more often tapering to end), ornamentation verruculose to verrucose except on smooth apical callus and eccentric apiculus, suprahilar plage an indistinctly bordered area of lowered ornamentation (oil immersion); orangish amber in KOH (ochraceous in H_2O , based on examinations of paratypes). BASIDIA ($n = 19$): 4-spored, curved; broadly clavate above narrower base, $25\text{--}34.2\text{--}41(43) \times 6.5\text{--}8.1\text{--}9.4(9.9) \mu\text{m}$, sterigmata $2.0\text{--}3.0\text{--}3.7 \mu\text{m}$ long, curved; hyaline to dull orangish brown, guttulate, granular, or uniformly oily. CHEILOCYSTIDIA $24.2\text{--}28.7\text{--}34 \mu\text{m}$ long, diameters (basal septum) $2\text{--}2.6\text{--}3 \times$ (stomach) $4.9\text{--}5.7\text{--}6.9 \times$ (neck) $1\text{--}1.3\text{--}1.6 \times$ (capitulum) $1.5\text{--}2.0\text{--}2.6 \mu\text{m}$ ($n = 13$), abundant, intermixed with basidia, secretory; capitulate tibiiform (primarily) and lageniform, (only occasionally intermixed with thin-walled clavate elements), bases hyaline, necks and capitula refractive, thick-walled, pale amber. PLEUROCYSTIDIA absent except for isolated cheilocystidia scattered occasionally on the gill face. LAMELLAR TRAMA hyphae parallel, $65\text{--}80 \times 3\text{--}6 \mu\text{m}$, thin-walled, hyaline inflated, subgelatinized, narrowing toward gill edges to $2\text{--}3 \mu\text{m}$ diam and giving rise to the subhymenial layer. SUBHYMENIUM c. $25 \mu\text{m}$ thick, hyphae $2\text{--}4 \mu\text{m}$ diam, tightly packed, parallel, cylindrical, hyaline, gelatinized. PELLICULAR HYPHAE: PILEIPELLIS a bilaminate ixocutis with a $\geq 300 \mu\text{m}$ thick SUPRAPELLIS with elements tightly compact in freshly dried material (but readily separating in gel matrix after 11 years in fungarium), hyphae $>40 \times 1.5\text{--}5.0 \mu\text{m}$, radially aligned, sinuous, long-branching, gelatinized, frequently (spirally) gel encrusted, hyaline; SUBPELLIS c. $500 \mu\text{m}$ thick, gelatinized, vessel



A–C, E–G: Lorelei Norvell. D, H, J: Ron Exeter v. Heidi Christensen.

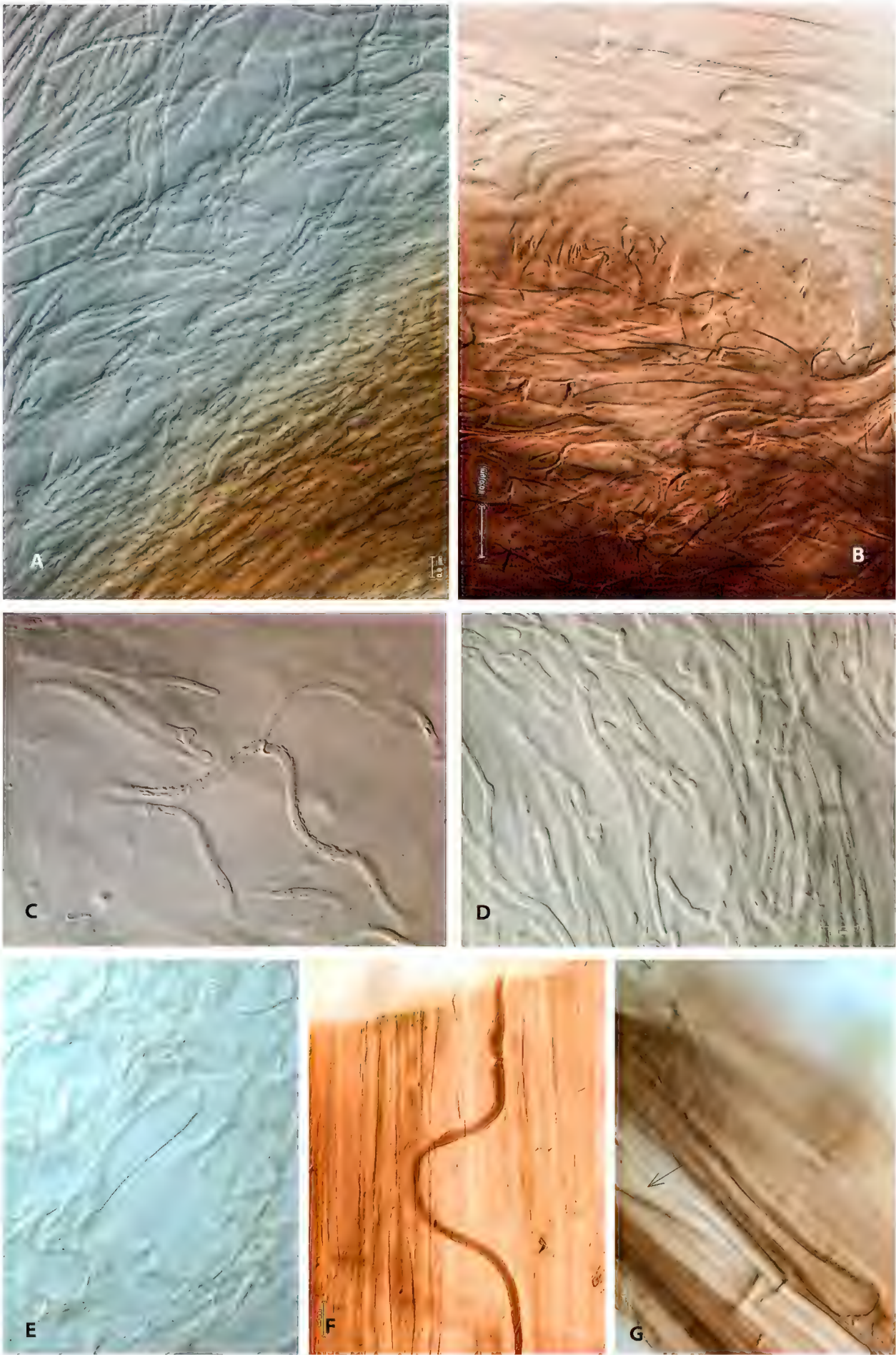
FIG. 4. *Phaeocollybia chefensis* paratypes. [Lincoln Co.: LLN1951109-16 (A–C), RLE2007-074 (F), RLE2015-21 (H), RLE2021-1 (J); Lane Co.: RLE2007-129 (D, E); Polk Co.: HC2018-LB4 (I); Benton Co.: LLN2091026cc6 (G)]. A–C. Three views of the first specimen from CHEF that fostered the concept for *P. tibiikauffmanii* in 1995. D. Young robust specimens excavated from Lobster Creek. E. Pristine pseudorhizal tissues display strong magenta reaction in syringaldazine after 15 minutes. F. Second specimen retrieved from CHEF in 2007. G. Solitary specimen retrieved from Conner's Camp on Marys Peak. H. Basidiome at the original CHEF site prior to excavation in 2015. I. The first primordium excavated with its more mature partner in 2018 at Boulder Creek. J. Exeter's 2021 negative syringaldazine reaction from this waterlogged solitary cautions that adverse environmental conditions do disable this usually reliable diagnostic tool.

hyphae with thinner walls; hyphae long, 4–12 μm diam at septa and inflating to $\leq 25 \mu\text{m}$; pigments orange to dark brownish orange, diffuse to occasionally encrusting, soluble in KOH (forming droplets in mountant); small hyaline crystals scattered infrequently throughout. STIPITIPPELLIS hyphae 75–100 $\times$ 1.5–3(6) μm , parallel aligned, gelatinized, pigments diffuse, pale amber to reddish in places. RHIZOPELLIS cells long $\times$ 4–10 μm , pale to dark amber, heavily gel- and/or red-brown pigment-encrusted. TRAMAL TISSUES: lightly (pileus) to noticeably (stipe, pseudorhiza) sarcodimitic, gelatinized, $\pm$ hyaline except darkening in pseudorhiza; VESSEL HYPHAE fusoid (sometimes tapering to obtuse end), 25–100 $\times$ 3–13 (at septa), rigid walls 1–2 μm thick; FLEXUOUS HYPHAE generally winding or curving around vessels, more or less cylindrical but sometimes appearing flattened, thin-walled, $\leq 50 \mu\text{m}$ long, diameters narrowest (1–2 μm) in pileus and broadest (3–5 μm) in stipe; OLEIFEROUS HYPHAE occasional to frequent in tramal tissues throughout, sinuous, aseptate, 3–10 μm diam, thin-walled, contents dull brown, oily. TIBIIFORM DIVERTICULA infrequent on aerial stipe apex, lageniform to (more often) tibiiform, frequent to abundant on rhizopellis, 8–20 μm long, 1–2 at base, narrowing in refractive neck area before expanding when capitula (1–2 μm diam) present; arising directly from hypha and lacking basal septum, secretory, hyaline, refractive to very pale amber. CLAMP CONNECTIONS absent in all tissues.

SYRINGALDAZINE SPOT TEST: strongly positive (pseudorhizal origin dark burgundy in five minutes; stipe (cross-section) and pileus and lamellae leaching magenta after ten minutes). FLUORESCENCE fresh material (of holotype) not tested; dried lamellae dull yellow orange (one small area of one specimen a brilliant orange yellow).

ADDITIONAL SPECIMENS EXAMINED—UNITED STATES, OREGON, Benton Co. Conner's Camp, 44.5060°N 123.5565°W, 762 m asl, 200yo PSME TSHE 26.x.2009 LLN2091026cc6 (MZ352101). Lane Co. Lobster Valley, 44.2268°N, 123.6148°W, 427 m asl, 200yo PSME young TSHE GASH, 6.xi.2007 RLE2007-129 (MZ352096). Lincoln Co. Cascade Head EF, 30 m S Tillamook Co. Line, 45.0447°N 123.9153°W, 245 m asl, ~120yo PISI TSHE VAPA POMU OXOR: 9.xi.1995 LLN1951109-19; 18.x.2007 RLE2007-074

FIG. 5. *Phaeocollybia chefensis* (Holotype, RLE2009-04): A. Colorless suprapellis in gelatinous matrix overlying a pigmented subpellis [400 $\times$]. B. Pileipellis under oil [1000 $\times$]. C, D. Suprapellis hyphae (gel encrustations detailed in C). E. Lightly sarcodimitic pileus tramal tissues with relatively thin-walled vessel hyphae. F. Oleiferous hyphae in stipititrama (just below pellis hyphae). G. Strongly sarcodimitic pseudorhizal trama with thick-walled vessel hyphae and thin-walled flexuous (arrow) hyphae.



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(MZ352097, KU574779); 2.xi.2015 RLE2015-21 (KX574495); 14.x.2021 RLE2021-01.
 Polk Co. Boulder Creek 44.8983°N 123.4995°W, 823 m asl, ~80yo ABPR PSME TSHE
 POMU VAPA 10.x.2018 HChristensen HC2018-LB4 (OSC 155803; MK326851).

ECOLOGY & DISTRIBUTION: autumn (October–November); basidiomes solitary or in pairs in needle duff under mature *Abies procera*, *Tsuga heterophylla*, *Picea sitchensis* and/or *Pseudotsuga menziesii* with understory of *Gaultheria shallon*, *Oxalis oregana*, *Polystichum munitum*, *Vaccinium ovatum*, and/or *V. parviflorum*. Known thus far from only five sites along the Oregon coast and in the Oregon coast range.

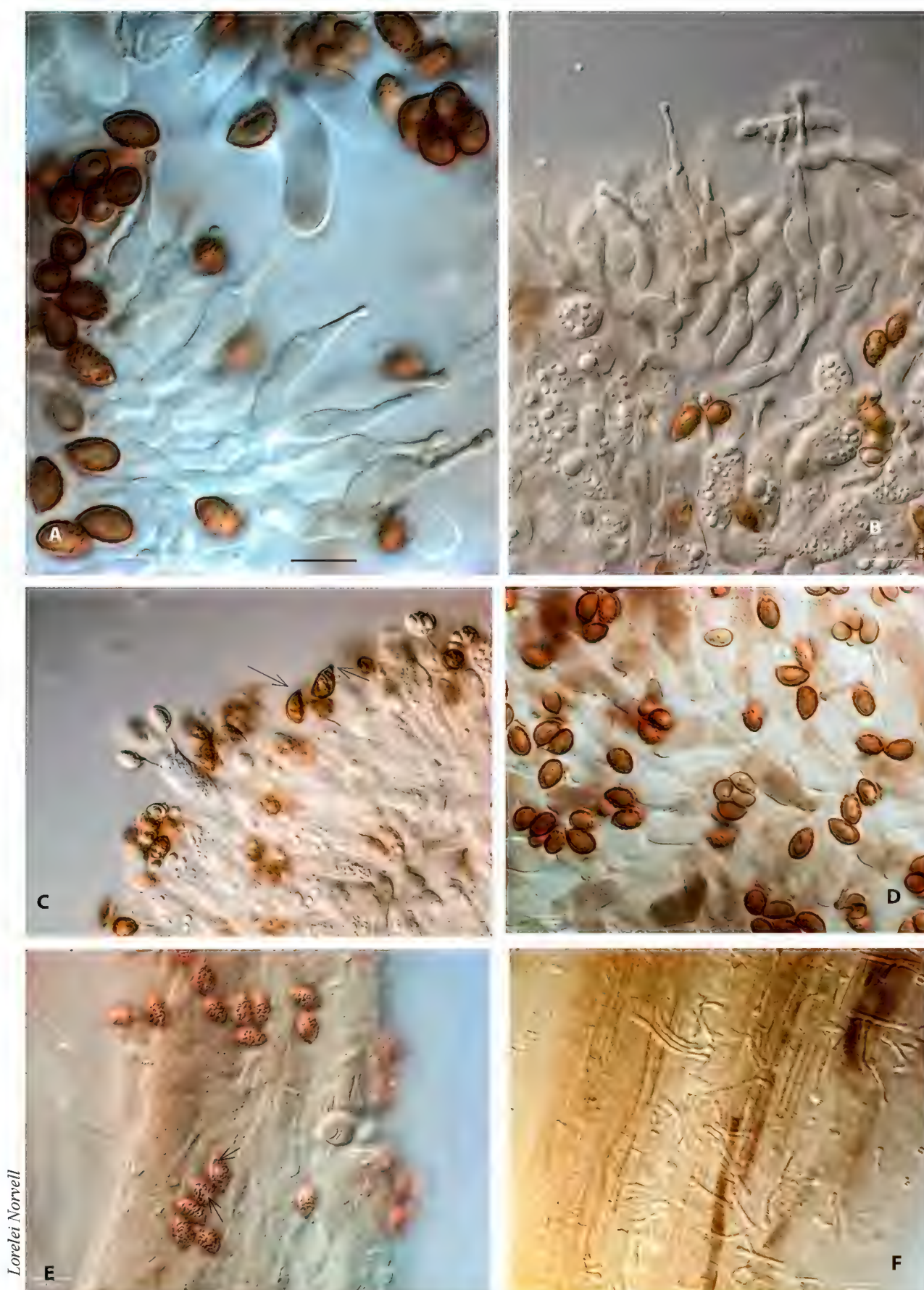
Discussion

Phaeocollybia chefensis

Diagnostic characters include a bright orange to brownish orange viscid conic-campanulate pileus, seemingly robust stature that in age becomes limp or flaccid, stuffed stipe, vertical monopodial pseudorhiza, medium-sized limoniform verrucose basidiospores, thick-walled tibiiform cheilocystidia, and lack of clamp connections. ITS and RPB2 sequence analyses strongly support *P. chefensis* as an independent species (FIGS 1, 2).

Morphologically, all paratypes match the type, except for the smaller (7.5–8–9 × 4–4.5–5.2 µm) basidiospores measured in the immature 1995 specimen (LLN1951109-19), which in part explains why Norvell (2004) did not detect the selection of a *P. spadicea* collection as type until after sequence analyses. The 1995 collection has not been sequenced, but sequences from the four subsequent collections from the identical site strongly support the earlier collection as *P. chefensis*. The molecularly confirmed collections imply *Tsuga heterophylla* as the primary ectomycorrhizal associate; possible secondary associates include *Picea sitchensis* at the type locality (245 m asl), *Pseudotsuga menziesii* at the Lobster Creek (427 m asl) and Conner's Camp (762 m asl) sites, and *Abies procera* and *Pseudotsuga menziesii* at Boulder Creek (823 m asl). Lamellae of fresh specimens examined under UV exhibited the strong yellow fluorescence characteristic of all PNW phaeocollybias except for the uniquely non-fluorescing *P. gregaria* A.H. Sm. & Trappe.

As noted above, *Phaeocollybia chefensis* closely resembles *P. kauffmanii* macroscopically, while microscopically it is quite similar to *P. spadicea* and *P. pseudofestiva* A.H. Sm., *Phaeocollybia chefensis* shares with *P. kauffmanii* a brownish orange viscid pileus, stuffed stipe, vertical-monopodial pseudorhiza, magenta syringaldazine reactivity, and morphologically similar basidiospores, but the presence of refractive thick-walled tibiiform cheilocystidia and



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Fig. 6 *Phaeocollybia chefensis* (Holotype, RLE2009-04 (A,D,E); RLE2007-074 (B,C); RLE2007-129 (A,B): A, B. Cheilocystidia. C. Granular basidia, sterigmata, and orangish brown basidiospores with smooth apical beaks (arrow). D. Basidiospores with older basidia lacking guttules or granules. E. Comparison of verrucose spore ornamentation and less ornamented plage regions (arrows). F. Abundant tibiiform diverticula on pseudorhizal pellis.

the absence of heavily gelatinized, strongly sarcodimitic elements in the stipe and less extensive gelatinous matrix in the suprapellis clearly separate *P. chefensis* from *P. kauffmanii*. In the field the much longer-lived *P. kauffmanii* can be distinguished by its larger (at times massive) and more robust stature, sharp farinaceous odor and taste, strongly inrolled mature pileus edge, and frequently gregarious habit.

Phaeocollybia spadicea, sharing many morphological features that led to the selection of an orange form as type for *P. tibiikauffmanii*, differs in its darker tawny (“date-colored”) to frequently blackish brown pileus, abundant rough fibrillose patches (invariably covered with tibiiform diverticula) on the stipe apex, closely gregarious habit, and (often) negative reactivity of the pileus and lamellar tissues to syringaldazine. Specimen age and condition may explain the variable syringaldazine reactivity in both *P. chefensis* and *P. spadicea*.

Phaeocollybia pseudofestiva, which shares general basidiospore and cheilocystidial morphology, syringaldazine reactivity, and odor and taste is easily separated from *P. chefensis* by its dark green pileus, smaller size, more prominently beaked basidiospores, cord-like pseudorhiza, and closely gregarious habit.

Phaeocollybia tibiikauffmanii* and *P. spadicea

As noted above, comparisons of ITS and RPB2 sequences from collections designated as either *P. spadicea* or *P. tibiikauffmanii* based on the presence/absence of orange coloration (Norvell 1998a,b,c, 2004; Norvell & Exeter 2009) revealed that all (including the holotype) except one (FIG. 3A) *P. tibiikauffmanii* collection represented *P. spadicea*. Subsequent morphological comparisons have shown that *P. spadicea* pileus colors range along a foxy orange to tawny to deep brown continuum. Additionally, all seven *P. chefensis* collections occurred singly or in pairs in contrast to *P. spadicea*, which typically occurs in closely gregarious to cespitose clusters; Alexander Smith’s notes archived in MICH describe an “orange” *spadicea* that he provisionally named *P. “caespitosa”* (a name he also provisionally applied to what was to become *P. scatesiae* A.H. Sm. & Trappe; Norvell 1995). Thus, we propose the synonymy:

***Phaeocollybia spadicea* A.H. Sm., Brittonia 9: 215, 1957.**

FIG. 5

= *Phaeocollybia tibiikauffmanii* Norvell, Mycotaxon 90: 248, 2004.

SPECIMENS CONFIRMED AS *Phaeocollybia spadicea* (listing those previously cited as *P. tibiikauffmanii* in Norvell (2004) and/or Norvell & Exeter (2004, 2009)—UNITED STATES. OREGON: Benton Co. Conner’s Camp 44.5060°N 123.5565°W, 762 m asl,

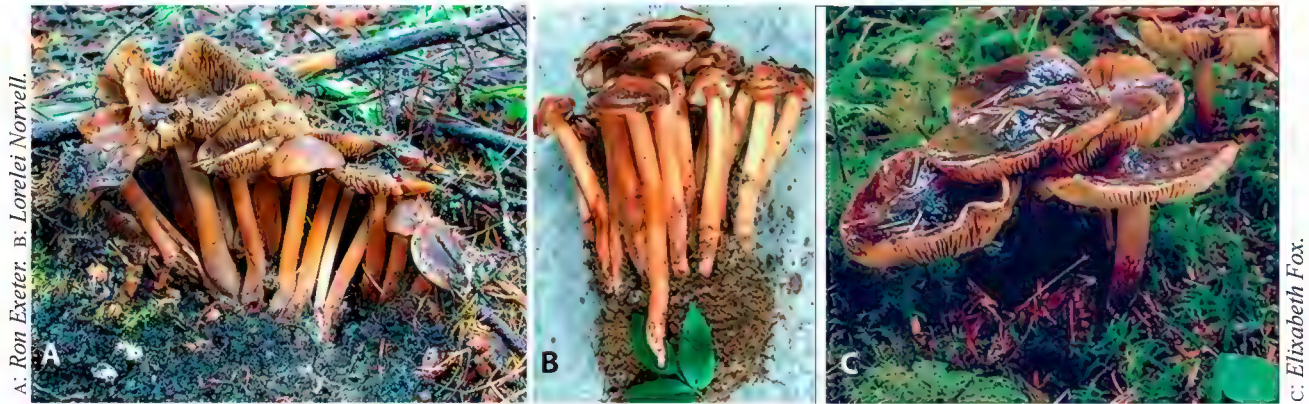


FIG. 7. *Phaeocollybia spadicea* [RLE208-55 (A); A2011031o2-1 (B); LLN1921015-10 (C)]. A. Gregarious cluster on Oregon's Marys Peak (as *P. tibiikauffmanii* in Norvell & Exeter 2009). B. Excavated *P. tibiikauffmanii* holotype from the Polk County Chronosequence Study. C. "Typical" brown-capped *P. spadicea* specimens in Hoh Valley, Olympic National Park.

200yo PSME TSHE, 5.xi.2005 RLE2008-55 (KF219592); Ernest Creek 44.4185°N 123.5165°W, 610m asl, 200yo PSME TSHE 15.xi.2007 RLE2007-165 (KU574777, KF219594); Running Bear 44.4774°N 123.5769°W, 696 m asl, 60yo PSME TSHE, 6.xi.2000 DCalver RLE200-103 (KF219595). Polk Co. Pedee Chronosequence Study 44.8113°N 123.5212°W, 460 m asl, 150yo PSME TSHE POMU 4.xi.1998 (all by LLN & RLE) A1981104o1-01, A1981104o2-02-04 (with CHibbler); 5.x.2000 RLE200-045; 18.x.2000 A2001018o1-15,o2-25; 1.xi.2000 RLE200-091, A2001101o2-30; 31.xi.2001 A2011031ox1 (*P. tibiikauffmanii* holotype; KF219597, KU574780), A2011031o2-03,04,05,06,08, A2011031ox-02; 14.xi.2011 A2011114o1-01,02,03, A2011114ox-01; 15.x.2002 A2021015o2-01; 13.xi.2002 A2021113o2-01,02,03; 14.xi.2006 A2061114o2-O (KF219596, KU574778), RLE2006-47, 16.x.2007 rle2007-060 (KF219593). WASHINGTON: Jefferson Co. Hoh Valley @ Twin Creek 47.8307°N 124.0012°W, 180 m asl, ~400yo PISI TSHE POMU OXOR 15.x.1992 LLN1921015-10_{spds1} (w SAR) (WTU-F-003698; previously cited and RFLP-confirmed as *P. spadicea*).

ADDITIONAL EXAMINATION NEEDED BUT PROBABLY ALSO *Phaeocollybia* P. —UNITED STATES. OREGON: Benton Co. Green Peak BLM Density Management Study 44.366°N 123.455°W, (all GP collections by LLN & RLE): Clear-cut transect (pre-treatment)—610m asl, 65yo PSME TSHE POMU 24.xi.1998 GP1981124c1-04 (w TFennell); High Retention transect 579m asl, 65yo PSME TSHE POMU— 8.xii.1999 GP1991208hx.03 (w SAR) (PNW, DAOM), 27.xi.2000 GP2001127hx3; Klickitat BLM Unit-3 44.4406°N 123.5673°W, 60yo PSME TSHE GASH 30.x.2000 RLE200-065; 16.xi.2000 RLE200-252; Klickitat Unit-6 T.S. 44.4548°N 123.5473°W, 50yo PSME TSHE POMU: 30.x.2000 RLE200-082,83,90, 14.xi.2000 RLE200-187b; 44.4260°N 123.5472°W, 60yo PSME TSHE GASH: 30.x.2000 RLE200-070; RUNNING BEAR T.S. 44.4774°N 123.5770°W, 200yo PSME TSHE POMU 9.xi.1998 LLN1981109.108e w RLE, 6.xi.2000 RLE200-103; 28.x.2002 RLE2002-16. Linn Co. Keel Flats T.S. 44.5133°N 122.6518°W, PSME BENE POMU 6.xii.1999 KScott RLE199-BK. Polk Co. Pedee Crk head waters near Cold Springs 44.8233°N 123.4862°W, 610m asl, 200yo PSME TSHE GASH 26.xi.2001 RLE 2001-112,115. WASHINGTON: Clallam Co. Olympic NF Klahanie Campground 47.9657°N 124.3057°W, 250yo PISI TSHE 18.x.1992 STrudell LLN1921018-4_{usps3} (WTU-F-003646).

Phaeocollybia rufotubulina* and *P. californica

On November 16, 1992, numerous densely gregarious orange phaeocollybias in Jackson State Forest (Mendocino County, California) were collected and referred to *P. californica*. This first highly informative collection contained numerous pin-head primordia that helped establish the presence of a universal veil for all *Phaeocollybia* species and introduced the ‘sequential-racemose’ pseudorhiza arising from a horizontal ‘mother rhizomorph’ within the soil (Norvell 1998b, 2004).

Restriction Fragment Length Polymorphism (RFLP) analyses of the ITS region from type materials supported separation of *P. rufotubulina* from *P. californica* and *P. scatesiae* (Norvell 1998a), indicating a new species and supporting the synonymy of *P. scatesiae* under *P. californica* proposed by Horak (1977). The 2009 ITS sequence analyses, however, clustered *P. californica* and *P. rufotubulina* within one intermixed clade well-separated from *P. scatesiae*, a brownish species macroscopically easily distinguishable in the field from the two orange phaeocollybias. *Phaeocollybia scatesiae* is now supported as independent from *P. californica* (FIGS 1,2).

Given the difficulty encountered in isolating DNA from the *P. californica* holotype (obtained in 2011), it is probable that the 58-year-old *P. californica* DNA isolated in 1994 was contaminated by DNA isolated in the same run from the much younger *P. scatesiae* isotype. We hereby propose the synonymy:

Phaeocollybia californica A.H. Sm., Brittonia 9: 216, 1957.

= *Phaeocollybia rufotubulina* Norvell, Mycotaxon 90: 243, 2004.

Norvell & Exeter (2009) presented *P. californica* (pp. 63–70) and *P. rufotubulina* (pp. 175–180) as separate species; all material related to *P. rufotubulina* throughout that monograph as well as those in Norvell (1998a,b, 2004) should now be referred to *P. californica*.

Phaeocollybia riffliipes* and *P. lilacifolia

During a two-month long collecting expedition through western North American coastal rainforests 1992, several small lilac-gilled tawny to dark brown-capped phaeocollybias were collected and provisionally determined as *P. lilacifolia*. Except for flaccid small basidiomes and unusually small basidiospores, the specimens morphologically matched Smith’s *P. lilacifolia* type from Washington’s Mt. Rainier Park (Smith 1957a). However, 1994 restriction digests produced a RFLP profile unique to these collections. Unable to extract DNA from the Washington *P. lilacifolia* holotype or Smith’s

Cascade Head Experimental Forest paratype, Norvell (1998a, 2002) proposed the name *P. riffripes* (honoring its unique RFLP fingerprint) for the specimens that were morphologically separated by unusually small basidiospores and stature.

During 2001–2013, numerous small *P. riffripes* specimens were collected from the Polk County old growth chronosequence transect; not until 2007, however, was the first recognizable *P. lilacifolia* collected from Lincoln County’s Saddle Bag Mountain, c. 25 km southeast of Cascade Head Experimental Forest. The Saddle Bag collections comprised robust healthy specimens with normal-sized basidiospores. In 2009, ITS phylogenetic analyses clustered *P. lilacifolia* sequences and all but one *P. riffripes* sequences within one clade, a clade supported by our current ITS and RPB2 phylogenies. Disposition of 4592sl (MZ352100), a Loring collection from Josephine County (initially identified as *P. riffripes*), remains unresolved at this time.

Although we have not yet successfully isolated DNA from Smith’s *P. lilacifolia* holotype or paratypes, the small “limp” stature, poor condition, and age of the 1992–1994 collections suggest that their peculiar RFLP profiles resulted from an unknown contaminant. The following synonymy is proposed:

Phaeocollybia lilacifolia A.H. Sm., Sydowia Beih. 1: 59, 1957.
= *Phaeocollybia riffripes* Norvell, Mycotaxon 81: 102, 2002.

All keys, descriptions, and photos of *P. riffripes* in Norvell (1998a, 2002) and Norvell & Exeter (2009) should be referred to *P. lilacifolia*.

Revised general key to Pacific Northwest *Phaeocollybia* species

Basidiospore size ranges of measurements taken from holotype specimens are cited for species; means of measurements taken from molecularly confirmed specimens are cited for complexes.

- 1. Basidiomes small: pileus ≤50 mm diam, and never green or drab;
 stipe apex usually ≤4 mm diam and never drab 2
- 1. Basidiomes medium to large: pileus usually ≥50 mm diam;
 stipe apex usually >5 mm diam 5
- 2. Basidiospores ellipsoid, ornamentation minutely punctate and
 small apical callus detectable in 1000× oil immersion;
 clamp connections present 3
- 2. Basidiospores limoniform, ornamentation verrucose and
 protruding apical beak visible without oil immersion lens;
 clamp connections absent 4

- 3. Spores small ($5-6 \times 3-3.5 \mu\text{m}$); cheilocystidia lageni-/tibiiform, necks narrow and thick-walled, abundant but inconspicuous, difficult to see in dense gelatinous matrix; basidiome collybioid, stipe pliable *P. radicata*
- 3. Spores larger ($\sim 10 \times 6 \mu\text{m}$); cheilocystidia thin walled, narrowly clavate, extending well beyond hymenium; basidiome mycenoid, stipe fragile and easily broken ... *P. phaeogaleroides* complex
- 4. Stipe and pseudorhiza fleshy, not shiny or brittle; cheilocystidia tibiiform, necks and capitula refractive and thick-walled; pleurocystidia present and, frequent on gill faces; spores $8-11 \times 5-7 \mu\text{m}$, tapering to straight beaks; phenology vernal *P. pleurocystidiata*
- 4. Stipe polished, corneous, soon hollow; pseudorhiza lateral monopodial, brittle and wire-like (criniform); cheilocystidia clavate, thin-walled; pleurocystidia absent; spores $7-8.5 \times 5-5.5 \mu\text{m}$, big-bellied with abrupt tilted beaks; phenology autumnal *P. attenuata*
- 5. Young pileus green, rapidly aging to brown or brownish olive 6
- 5. Young pileus ochre, orange, tawny, brownish, or drab (never green) 8
- 6. Young lamellae violet; spores $\sim 9 \times 5.3 \mu\text{m}$, moderately beaked, in face view fusoid or naviculate, verrucose to marbled; cheilocystidia clavate, thin-walled, apices swollen to subcapitate, only rarely forming filiform apical outgrowths *P. fallax* complex
- 6. Young lamellae creamy to yellowish buff; spores limoniform with pronounced beak, +/- ovate in face view, rugulose to warty roughened; cheilocystidia clavate or tibiiform 7
- 7. Spores $7.5-8 \times 4.5-5 \mu\text{m}$, with long, projecting beaks; cheilocystidia tibiiform with narrow refractive necks *P. pseudofestiva*
- 7. Spores $\sim 10 \times 6 \mu\text{m}$, 'turtle-backed' with abruptly protruding eccentric refractive beaks; cheilocystidia thin-walled, clavate, filiform apical outgrowths frequent in age *P. olivacea* complex
- 8. Spores ellipsoid, short ($<7.5 \mu\text{m}$), punctate-roughened; cheilocystidia clavate, thin-walled 9
- 8. Spores limoniform, verruculose to warty; cheilocystidia tibiiform or clavate 11
- 9. Basidiome drab to gray, robust; stipe ≤ 20 mm diam, stout, firmly stuffed; pseudorhiza fleshy; taste and odor cucumber-farinaceous; spores $6-7.5 \times 4-4.5 \mu\text{m}$; all tissues soon deep magenta in syringaldazine *P. oregonensis*
- 9. Basidiome orange to auburn colored, fragile; stipe ≤ 13 mm diam, slender, hollow; pseudorhiza cord-like; taste and odor mild; pileus & lamellae syringaldazine negative 10

10. Clamp connections abundant; pileus orange with yellowish margin,
viscid, conic-campanulate; cheilocystidia filamentous to narrowly clavate;
spores $5.5\text{--}6.5 \times 3.5\text{--}4.3 \mu\text{m}$ *P. dissiliens*
10. Clamp connections absent; pileus uniformly auburn colored,
subviscid, campanulate with a raised blunt umbo;
cheilocystidia narrowly clavate with long pedicels and subcapitate apices;
spores $5.5\text{--}6.5 \times 3\text{--}4 \mu\text{m}$ *P. sipei*
11. Pileipellis 3-layered with colorless gelatinized middle layer
between yellow to yellow-orange top and bottom layers;
pileus minutely scaly (appressed), dry to subviscid (never glutinous) 12
11. Pileipellis 2-layered, with colorless top layer and variously pigmented lower layer;
pileus bald, smooth (never appressed scaly), subviscid to glutinous 13
12. Spores large, $9\text{--}11 \times 5\text{--}6.8 \mu\text{m}$;
pileus dry to greasy, yellowish ochre to ochraceous gold;
frequently associated with *Abies* *P. luteosquamulosa*
12. Spores smaller, $7.2\text{--}8.7 \times 4.4\text{--}5.5 \mu\text{m}$;
pileus greasy to subviscid, tawny ochraceous or tawny;
associated with *Pseudotsuga* or *Tsuga* *P. ochraceocana*
13. Cheilocystidia tibiiform, broad bases thin-walled,
capitula and narrow necks refractive and thick-walled;
stipe hollow or stuffed 14
13. Cheilocystidia variably cylindrical to clavate,
filamentous apical secondary growth occasional in older specimens
but always lacking refractive thick-walled necks;
stipes stuffed with firm pith 17
14. Mature stipe tubular and hollow; basidiomes closely gregarious to fasciculate,
arising from a branching rhizomorphic cord 15
14. Mature stipe stuffed with firm compact pith; solitary to closely gregarious,
arising from unbranched fleshy (not cord-like) pseudorhiza 16
15. Pileus heavily glutinous, acutely conic-campanulate, yellowish to dark brown;
habit in dense fasciculate mounds; suprapellis thick, colorless,
hyphae kinked, not spirally pigment-encrusted and with septa obscured
by thick gel matrix; spores $8.5\text{--}9.5 \times 4.5\text{--}5.5 \mu\text{m}$ *P. scatesiae*
15. Pileus moist to viscid, obtusely convex-campanulate, red orange to tawny;
habit in troops, arcs, or (rarely) fasciculate mounds; suprapellis compact,
amber to orange, hyphae spirally pigment-encrusted with refractive septa;
spores $8.5\text{--}10 \times 5\text{--}6 \mu\text{m}$ *P. californica*
16. Pileus foxy orange to orangish brown; stipe apex orange cinnamon colored;
habit solitary or paired, never gregarious; all tissues soon magenta in
syringaldazine; spores $8\text{--}10 \times 5\text{--}5.8 \mu\text{m}$ *P. chefensis*
16. Pileus tawny to dark brown; stipe apex pallid to drab;
habit gregarious to fasciculate; only pseudorhiza magenta in
syringaldazine; spores $7.5\text{--}9 \times 4.5\text{--}5 \mu\text{m}$ *P. spadicea*

- 17. Clamp connections frequent throughout, most easily seen
in pileus suprapellis and on cheilocystidia;
pileus campanulate with often papillate umbo, tawny ochraceous to tawny;
cheilocystidia cylindrical to narrowly clavate;
spores $8.4\text{--}9.2 \times 5\text{--}6 \mu\text{m}$ *P. ammiratii*
- 17. Clamp connections lacking (rarely in stipitipellis);
pileus shape & color, cheilocystidial shape, and spore size varied 18
- 18. Young lamellae whitish, smoky gray, or deep violet;
young pileus colors tawny, brownish-pink or drab;
pileus and lamellae magenta in syringaldazine 19
- 18. Young lamellae pinkish, orangish, or yellowish;
young pileus colors rarely pink or drab;
syringaldazine reactivity varied 20
- 19. Spores $7.5\text{--}9.4 \times 4.5\text{--}5.5 \mu\text{m}$; young lamellae intensely bluish lilac to violet;
pileus tawny to deep brown; taste not distinctive;
pseudorhiza syringaldazine negative *P. lilacifolia*
- 19. Spores $9 \times 5.5 \mu\text{m}$;
young lamellae white (pinkish) or ash gray, never lilac or violet;
pileus pinkish, drab, or purplish brown; taste 'bitter-cucumber' farinaceous;
all tissues soon deep magenta in syringaldazine *P. benzokauffmanii*
- 20. Young lamellae never fluorescing under UV;
pileus yellow tan, soon darker (cocoa brown); young stipe ivory tan,
lower stipe staining orange or orange banded at ground level;
habit densely gregarious; syringaldazine negative;
spores $9\text{--}10 \times 4.5\text{--}6 \mu\text{m}$ *P. gregaria*
- 20. Young lamellae fluorescing under UV;
pileus orange or tawny; young stipe apex buff, orange, or pale cinnamon,
lower stipe colors similar to apex, habit scattered to gregarious,
syringaldazine negative or positive; spores $8\text{--}12 \mu\text{m}$ long 21
- 21. Basidiome small to moderately large; stipe apex ≤ 12 mm diam (slender),
stipe stuffed but larval infested, leaving a hollow rind at ground level;
pileus conic umbonate, subviscid, uniformly bright apricot-/peach-colored;
all tissues negative in syringaldazine; pileipellis hyphae colorless,
spirally gel-incrusted, subpellis pigments KOH soluble, diffuse;
spores $8\text{--}9.5 \times 5\text{--}6 \mu\text{m}$, beaks short ($\leq 5 \mu\text{m}$), straight *P. piceae*
- 21. Basidiome large to massive; stipe apex $10\text{--}25$ mm diam (robust),
stipe long-lived, stuffed with firm, insect-free pith;
pileus campanulate with obtuse umbo, viscid to glutinous, orange to tawny;
all tissues strongly magenta in syringaldazine;
pileus subpellis pigment-encrusted, pigments not KOH soluble;
spores with slightly tilted long ($\leq 1.5 \mu\text{m}$) beaks 22

22. Spores 7.5–10 × 4–6 µm, limoniform, beak forward-tilted;
pileus +/- uniformly orange, tawny, or orangish brown,
typically drying with a burgundy-colored peaked umbo;
lower stipe and pith staining first orange, then orangish brown;
cheilocystidia cylindrical or narrowly to broadly clavate,
rarely pedicellate and subcapitate *P. kauffmanii*
22. Spores 8.5–12 × 5–7 µm, amygdaliform with long ‘belly’, beak back-tilted;
young pileus with reddish tawny umbo, amber margin, and tan edge,
eventually uniformly mahogany or dark reddish brown;
lower stipe and pith staining reddish brown;
cheilocystidia clavate to subcapitate with subglobose apices,
pedicellate, catenulate *P. redheadii*

Research on Pacific Northwest phaeocollybias is ongoing; a fully revised second edition of *PHAEOCOLLYBIA* OF PACIFIC NORTHWEST NORTH AMERICA will be released after several additional taxa have been published.

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